

Neural hemispheric organization in successful adult language learning: Is left always right?

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Abstract

Learning a new language during adulthood is a markedly difficult and heterogeneous process. Whether language learning engages the same left-lateralized language network as native language processing or a more distributed network is currently unknown. One approach to address this question is to evaluate the contributions of each cerebral hemisphere in successful language learning. The current review adopts an individual difference approach and provides a systematic overview of (1) the neural factors that

predict various language learning outcomes and (2) neuroplastic effects of successful language learning. Our analysis shows that, prior to learning, the neural characteristics of the left hemisphere predominantly predict future speech sound learning. However, more higher-level learning tends to be predicted by a more distributed network including the right hemisphere and bilateral brain structures. Over the course of language learning, both hemispheres show structural and functional malleability. We argue that a dynamic bilateral framework involving neural correlates both within and between the two hemispheres underlies the ultimate success of language learning. Learners' native language network (the leftward functional organization for language processing) is related to learning success at the speech sound and word levels. However, when learning involves greater complexity, the initial recruitment of the right hemisphere and the subsequent functional shift from right to left and bilateral hemispheres are essential to ensure successful attainment.



1. Introduction

Decades of research on first language acquisition and native language processing shape the contemporary neural frameworks of human language. The majority of the models for speech sound perception, language comprehension, and language production presume strong functional asymmetries, in which the left hemisphere compared to the right hemisphere exhibits a more widely distributed and more engaged language network (Friederici, 2009; Friederici & Alter, 2004; Hickok & Poeppel, 2004, 2007; Petersson & Hagoort, 2012). However, language learning in adults presents an entirely different landscape of research problems. Adult brains are far from being a *tabula rasa* when learning new languages. Lifetime experiences in perception and communication offer learners a set of sophisticated meta-linguistic skills and domain-general cognitive skills (e.g., working memory and cognitive control). Moreover, a mature brain that supports novel language experiences is simultaneously rewired by such learning experiences, adding complexity into the cascade of neural plasticity. In particular, many questions regarding language learning and the brain remain, including whether the left hemisphere still primarily houses the neural signatures of successful language learning in adults, as opposed to the right hemisphere. These questions gain particular significance when we consider the fact that the world is predominantly bilingual. Importantly, the bulk of the studies geared toward identifying hemispheric involvement in bilingual language use have examined lifelong bilinguals. Many studies have emphasized that

authors should take into account the fact that language learning ability and processing has been shown to differ across individuals based on the age of acquisition (AoA) ([Johnson & Newport, 1989](#); [Lenneberg, 1967](#)).

Thus, there is a large gap in the literature concerning the neural reorganization that occurs as adults begin to learn a new language. One of the main challenges that may have contributed to a lack of systematic examination of laterality across language learners is the fact that there is a high degree of variation in language learning ability across adult learners. One way to address this variation is to take an individual difference approach to investigate which elements of neural activity, structure, and connectivity are associated with differences in language learning ability. Therefore, this chapter reviews the most recent cognitive neuroscience evidence on individual differences in adult language learning success in order to gain a more comprehensive understanding of the nature of hemispheric asymmetries in language.

1.1 A brief historic overview of hemispheric dichotomy in language

One of the key questions concerning the relationship between the brain and cognition has been whether information is processed through a holistic whole-brain process or through the cooperation of specialized brain structures. So far, evidence from various facets of research indicate that the latter is more likely the case (see [Hugdahl & Westerhausen, 2010](#)). After all, the brain tends to process information in the most efficient manner possible. Having specialized brain areas for certain functions allows for faster processing speed. Some of the most striking evidence supporting the idea of specialized brain functions comes from the language literature, emphasizing a critical role of the left hemisphere in language comprehension and production.

Neuropsychology studies tracing back to the 19th century presented the earliest functional anatomical framework for language. Focal lesion at Broca's area, localized in the left inferior frontal gyrus (IFG) and Wernicke's area, localized in the left posterior superior temporal gyrus (STG), led to loss of function in speech production and comprehension, respectively ([Geschwind, 1970](#); [Lichtheim, 1885](#); [Wernicke, 1874](#)). Lesions at the right-hemisphere homologues, however, left most basic language functions of the patients intact and only affected higher-level meaning processing, such as pragmatic language use and non-literal language

processing (Brownell, Michel, Powelson, & Gardner, 1983; McDonald & Pearce, 1996; Weylman, Brownell, Roman, & Gardner, 1989; Winner, Brownell, Happé, Blum, & Pincus, 1998).

Since then, this simplified model has evolved substantially to refine the functional architecture of the left-hemisphere language network, which now includes a much wider range of brain areas and multiple neural pathways (Hickok & Poeppel, 2007; Martin, 2003; Price, 2000). Converging evidence from cognitive neuroscience studies highlight the involvement of the left hemisphere in various facets of language processing. In particular, a large proportion of functional magnetic resonance imaging (fMRI) studies indicate that structures comprising left frontotemporal and frontoparietal networks underlie processing and retrieval of phonological, semantic, and syntactic information (Friederici & Alter, 2004; Price, 2010). Conversely, the right frontal region's participation in these tasks are found to be limited, especially for articulation, phonological processing, and syntactic parsing (Friederici & Alter, 2004; Hickok & Poeppel, 2007; Price, 2000; Vigneau et al., 2011). An important consideration to make, however, is the fact that while many studies find left hemisphere rather than right homologue activation, few directly address the degree of lateralization or compare brain activation between the two hemispheres. Therefore, we cannot assume that a lack of right hemisphere findings necessarily indicates a greater involvement of the left hemisphere across all types of language processing. In fact, evidence from magneto/electroencephalogram (M/EEG) and fMRI studies suggest that the right temporal cortex is actively engaged in speech perception and is specialized in analyzing slow temporal variations in speech (e.g., prosody, pitch contour, and speech envelope) (Abrams, Nicol, Zecker, & Kraus, 2008; Jamison, Watkins, Bishop, & Matthews, 2006; Luo et al., 2006; Nan & Friederici, 2013).

It is worth noting that the studies reporting positive findings in the right hemisphere often focus on certain aspects of language, such as speech perception and semantic processing. For example, the mismatch negativity (MMN), an auditory component indexing the detection of a change in, or violation of, an automatically formed representation in auditory sensory memory, is reported to be largest over the left hemisphere for phonological variations and largest over the right hemisphere for non-linguistic acoustic variations. Yet this laterality effect might be modulated by a number of methodological factors, such as task demands or background noise (Bishop, 2007; Shtyrov et al., 1998; Uther, Jansen, Huottilainen, Ilmoniemi, & Näätänen, 2003). Studies using the half visual-field presentation technique, wherein visual stimuli are presented only to the left visual hemifield

(transmitted initially and preferentially to the right hemisphere) or right visual hemifield (transmitted to the left hemisphere) are uniquely positioned to examine hemispheric differences in various aspects of language comprehension. Studies using this technique indicate that both hemispheres are able to process fine-grained semantic information from words and sentences, a function previously thought to arise from mechanisms in the left hemisphere. However, compared to the right hemisphere, the left hemisphere was found to be dominant when it came to predicting upcoming words (see [Federmeier, 2007](#) for a review).

The neural architecture of the language network studied during the past 10 years embraces individual differences in brain functions, the many-to-many relationship between brain structures and functions, and the dynamic interplay between language and domain-general cognition ([Blumstein & Amso, 2013](#); [Fedorenko, Hsieh, Nieto-Castañón, Whitfield-Gabrieli, & Kanwisher, 2010](#); [Fedorenko & Thompson-Schill, 2014](#); [January, Trueswell, & Thompson-Schill, 2009](#); [Novick, Kan, Trueswell, & Thompson-Schill, 2009](#)). The left hemisphere dominance of native language processing, nonetheless, is seldom the center of the debate. By contrast, the right hemisphere's unique contributions are less stable and, for some functions such as production, are thought to be more limited.

1.2 Individual variations in adult language learning success

Language learning during adulthood compared to childhood is notoriously more difficult ([Newport, 1990](#)). The challenges appear to be universal across all aspects of language, including speech sounds, vocabulary, grammar, and ultimately the overall language proficiency. The capacity to discriminate non-native speech sounds fades during early development. Infants go through a “perceptual narrowing” phase before their first birthday, when they become increasingly more tuned to native speech sounds and less tuned to foreign speech sounds ([Kuhl et al., 2008](#); [Werker & Hensch, 2015](#)). Adults seem to preserve some degree of sensitivity to non-native speech sounds, as evidenced by laboratory-based training studies finding widely distributed learning outcomes across individuals after intensive training ([Chandrasekaran, Sampath, & Wong, 2010](#); [Myers, 2014](#); [Wong & Perrachione, 2007](#)).

Vocabulary learning during adulthood has also been shown to be markedly difficult, potentially owing to many contributing factors, including the lack of translation equivalents across certain languages ([Malt & Sloman, 2003](#)) and differences in phonological memory ([Baddeley, Gathercole, & Papagno, 1998](#); [Service & Kohonen, 1995](#)), and language training context

(Collentine & Freed, 2004; Lan, Fang, Legault, & Li, 2014; Milton & Meara, 1995). The most consistent findings were that there were large variances in L2 learning success in each of these learning contexts, with no single language learning context or methodology equally benefiting all individuals. Due to the vocabulary learning difficulties seen across adult learners, an increasing number of studies have been geared toward providing additional scaffolding and developing new technologies to aid the mass of students struggling to learn L2 vocabulary (see Lan, Chen, Li, & Grant, 2015 for a review).

Regarding grammar learning, a seminal study by Johnson and Newport (1989) provided the earliest evidence for a sensitive period for attaining second language grammatical abilities. English grammar abilities of native Chinese or Korean speakers were highly related to their age of arrival in the United States, but the individual differences in English grammatical skills were no longer explained by the age of arrival after puberty (Johnson & Newport, 1989). Using computational modeling and web-based grammatical assessments collected from a large population of native and non-native English speakers around the world, a recent study suggested a relatively stable grammatical learning ability until about 17.4 years of age, which then declines steadily afterward (Hartshorne, Tenenbaum, & Pinker, 2018). Both studies highlight the increasing difficulty of learning with age. These findings raise more questions regarding what factors beyond the AoA contribute to the individual variation in grammar learning success.

Decades of behavioral research have also examined the cognitive, motivational, and environmental influences on holistic language learning outcomes (Dekeyser, 2012; Linck et al., 2013; Sparks, 2012; Sparks, Patton, & Ganschow, 2012). The set of skills documented as potential building blocks for adult language learning aptitude ranges from linguistic-specific to domain-general skills, such as perceptual sensitivity (Chandrasekaran et al., 2010; Wong & Perrachione, 2007), executive functions (Linck et al., 2013), memory capacity (Ettlinger, Morgan-Short, Faretta-Stutenberg, & Wong, 2015; Wong & Ettlinger, 2011), and first language skills (Melby-Lervåg & Lervåg, 2011; Sparks, 2012). These behavioral findings imply a much wider brain network associated with adult language learning success that is beyond the traditional language regions associated with native language processing. The remaining questions are whether the left hemisphere also dominates the adult language learning process and whether neural diversity in the left hemisphere underlies the variations across learning outcomes.

1.3 Organization of the current chapter

The current chapter argues for a balanced contribution of both hemispheres in successful language learning. We surveyed longitudinal language training studies that used cognitive neuroscience measures both in the laboratory and in the classroom, aiming to provide a qualitative analysis of the laterality findings associated with adult language learning success. To narrow the search for articles to be included in the current study, we selected studies that specified language learning in adulthood and included both individual difference measures for language learning and mentioned their findings in terms of left, right, or bilateral hemispheres. Moreover, we only included studies using the following neuroimaging methodologies: diffusion tensor imaging (DTI), electroencephalography (EEG), functional (fMRI) and structural magnetic resonance imaging (sMRI), and magnetoencephalography (MEG). As a result, 60 studies were included in our analysis, with an additional 13 bilingual studies included for comparison in the plasticity section. We examined whether individual differences in language learning outcomes were explained by neural measures in the left or right hemispheres (see Fig. 1 for the overall distribution of the findings by research methods). In Boxes 1 and 2, we provide glossaries for the neural and behavioral language learning outcome measures used in this chapter.

Language learning is a dynamic process. What neural networks prepare adults for novel learning experiences and how the brain adapts to the

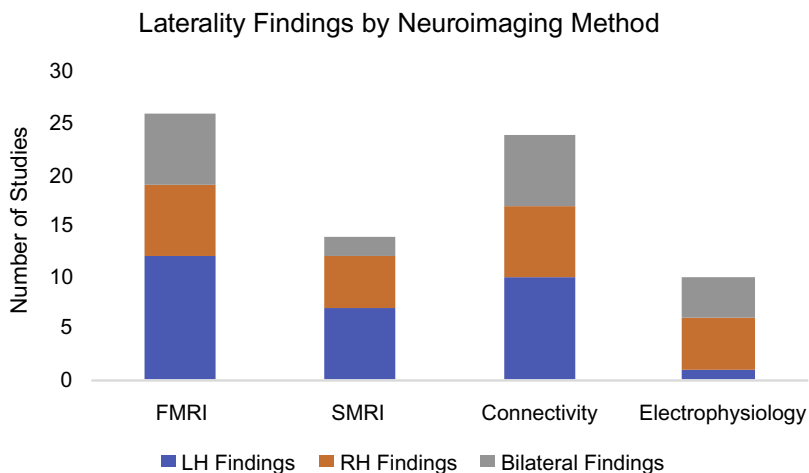
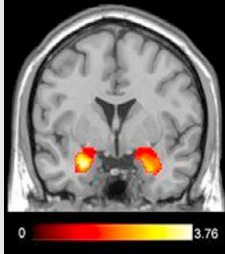


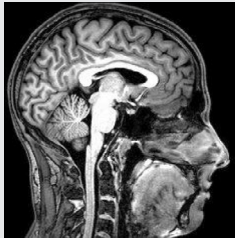
Fig. 1 Summary of the laterality findings for each neuroimaging methodology across all the language learning studies included in this review.

BOX 1 Glossary for Neuroimaging Measures



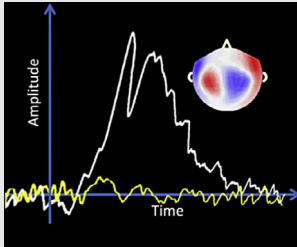
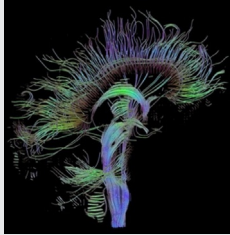
Functional Magnetic Resonance Imaging (fMRI) Measures

The Blood Oxygen Level-Dependent (BOLD) signal represents the ratio of oxygenated to deoxygenated blood in the brain and is a proxy measure for **neural activation** levels.



Structural Magnetic Resonance Imaging (sMRI) Measures

Cortical Thickness (CT) and **Gray Matter Volume (GMV)** are both measures of gray matter, which contains the dendrites and soma of neurons. Both CT and GMV reflect an aggregate measure of neural remodeling including axon sprouting, dendritic branching, and synaptogenesis. CT is defined as the distance between the gray matter (GM) and white matter (WM) boundaries along the surface of the brain, accounts for cortical folding along the surface of the brain, and can be measured at the submillimeter level. The GMV measure is limited by the size of voxel (usually 1mm or greater) used during data collection. **White Matter Volume (WMV)** is a measure of WM structure, which contains the axon fibers of neurons that connect regions of the brain.



Connectivity Measures

Functional Connectivity (FC) is measured using fMRI and is defined as the temporal correlation between the time series of neural activation across different brain regions. This remains true for both task-based FC and resting-state FC methodologies. Structural connectivity is measured via **Diffusion Tensor Imaging (DTI)**. Specifically, **fractional anisotropy (FA)** and **radial diffusivity (RD)** are two widely used measures for white matter microstructure. FA represents a normalized degree of unidirectionality of the movement of water molecules in the brain, while RD reflects the degree of diffusivity that is perpendicular to the main flow direction. A higher FA and a lower RD value denote greater WM connectivity.

Electrophysiology Measures

Event-Related Potentials (ERPs) are measured using electroencephalography (EEG) and represent the averaged electrophysiological response for a specific sensory, cognitive, or motor event. **Event-Related Fields (ERFs)** are measured via magnetoencephalography (MEG) and similarly represent the averaged electrophysiological response to a specific sensory, cognitive, or motor event. **Spectral Power** is measured via quantitative EEG (qEEG) and MEG, and reflects the number of neurons firing in synchrony.

BOX 2 Glossary for Language Learning Outcome Measures

Speech Sound Measures

This category includes measures of phonological encoding and discrimination. Specifically, this includes studies of linguistic tones, phonetic pitch contrasts, pitch detection, consonant identification, consonant categorization, and consonant imitations.

Word Measures

This category includes measures of encoding and retrieval of vocabulary items and includes learning of novel native language (L1) items, novel second language (L2) items, and pseudowords with or without associated meanings.

Reading Measures

This category reflects ability to integrate and comprehend visual linguistic information, and includes paragraph reading speed and passage reading fluency.

Grammar Measures

This category measures overall grammatic and syntactic ability, and includes studies using grammaticality judgment tasks, syntactic judgment tasks, artificial grammar tasks, grammatical production tests and grammatical comprehension tests.

Holistic Proficiency Measures

This category reflects holistic language performance, and includes course grades for language learning classes, scores on the Test of English for International Communication (TOEIC), general proficiency tests, combinations of sentence and vocabulary testing, the Hong Kong Certificate of Education Examination (HKCEE), the Hong Kong Advanced Level Examination (HKALE), and the International English Language Testing System (IELTS).

learning process are dependent on the types of language training. In [Sections 2 and 3](#), we will overview the laterality findings in terms of the acquired language skills of interest: speech sounds, words, grammar, reading, and the overall language proficiency. The current review first examines which pre-existing neural characteristics predict language learning outcomes. Then, we address which aspects of brain plasticity over the course of learning are associated with language learning outcomes. In [Section 3](#), we also gain insights from the findings from 13 bilingualism studies, where the brain measures in adults represent neural plasticity after lifetime experiences of learning and practicing two languages. In [Section 4](#), we highlight systematic individual differences in these findings and discuss their implications for hemispheric asymmetry in language.

2. Neural predictors of adult language learning success

Prior to starting a language learning program, adults are already equipped with different cognitive and neural profiles that may lead to disparate learning outcomes. The neural characteristics that prepare adults for effective learning result from individual differences in both traits and prior experiences. This section overviews the neural predictors of language learning (see [Box 1](#)) by categories of learning outcome measures (see [Box 2](#)). [Fig. 2](#) presents the overall pattern of laterality findings, where neural measures prior to training were related to longitudinal learning outcomes. The localizations of neural predictor findings from sMRI and fMRI studies are depicted in [Fig. 3](#) and those from the connectivity studies in [Fig. 4](#). Please note that a fair number of functional connectivity (FC) studies reported results based on pre-defined seed regions in the left hemisphere. Such analyses inevitably resulted in a left-lateralized pattern because regions in the right hemisphere would not be reported unless they were functionally connected to those in the left hemisphere. Overall, this body of literature suggests that neural features in the left hemisphere predominantly predict speech sound learning outcomes, but the right hemisphere plays an increasingly more important role as the outcome measure requires more sophisticated language skills (i.e., meaning, grammar, and holistic proficiency).

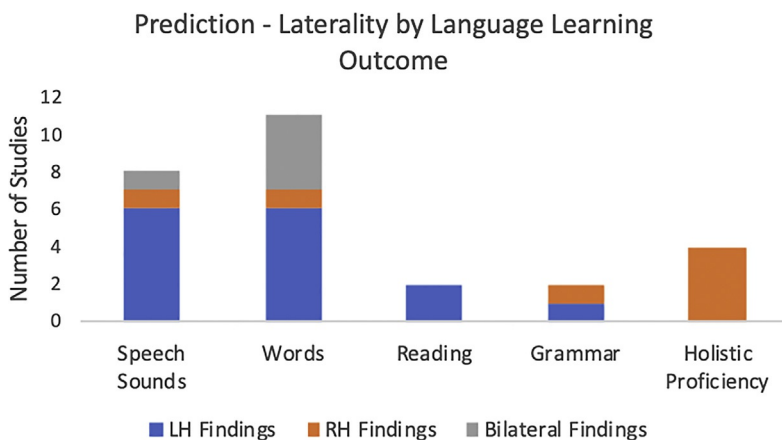


Fig. 2 Summary of the laterality findings for neural regions that predict language learning outcomes. Abbreviations: LH, left hemisphere; RH, right hemisphere.

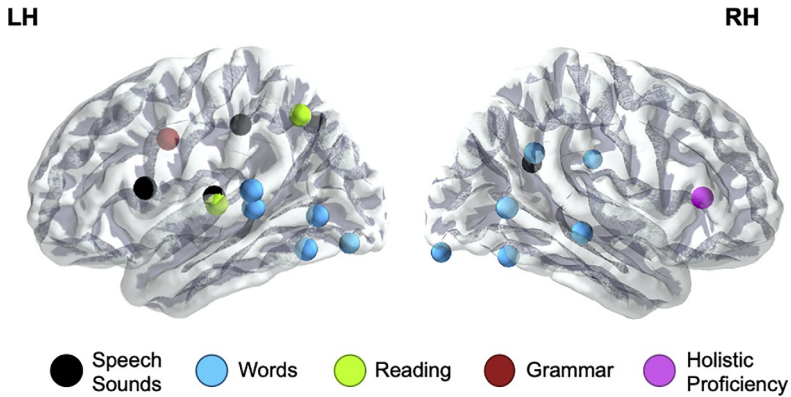


Fig. 3 Neural regions showing relationship between pre-training MRI measures and language learning outcomes. Abbreviations: LH, left hemisphere; RH, right hemisphere.

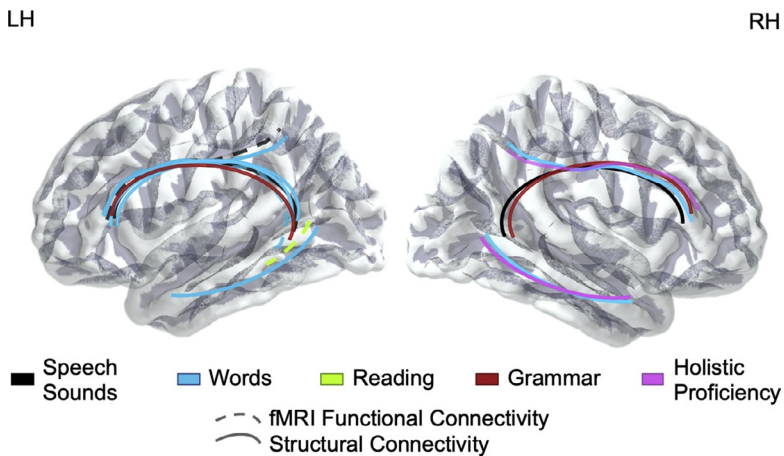


Fig. 4 Schematic showing the location of the connectivity findings in each hemisphere that predicted language learning outcomes. Abbreviations: LH, left hemisphere; RH, right hemisphere.

2.1 Neural predictors of speech sound learning success

The majority of studies investigating predictors of speech sound learning success found that brain regions located in the frontal, parietal, and temporal regions of the left hemisphere are positively related to how accurately learners identified and imitated foreign speech sounds. The involvement of the right hemisphere was reported in two studies, with one of them showing a negative correlation (Fig. 3).

The strongest evidence for the left-hemispheric bias in foreign speech sound learning comes from a series of studies examining the brains of native English speakers before they were trained on non-native Hindi dental-retroflex consonant contrasts. The white matter (WM) density of the parietal lobes bilaterally was found to be positively related to learning outcomes (Golestani, Paus, & Zatorre, 2002). However, comparing faster learners and slower learners, the authors found that faster learners had more prominent leftward asymmetry in Heschl's gyrus (HG) than slower learners. In contrast, slower learners compared to faster learners had greater gray matter (GM) and WM density in the right insula and parietal lobe (Golestani, Molko, Dehaene, LeBihan, & Pallier, 2007). Resting-state functional connectivity (rsFC) of the left frontoparietal network confirmed the functional relevance of the left hemisphere. FC between the left inferior frontal gyrus (IFG) and left parietal lobe prior to learning predicted better speech sound learning outcomes (Ventura-Campos et al., 2013).

Similar leftward asymmetry was reported in studies that investigate the production of foreign speech sounds in imitation tasks. The GM volume of the left IFG (Reiterer et al., 2011) and the structural connectivity of the left frontoparietal network, as measured by fractional anisotropy (FA) values in the left arcuate fasciculus (AF) (Vaquero, Rodríguez-Fornells, & Reiterer, 2017), were both associated with more accurate production of non-native speech sounds. Alternatively, the FA values in the right AF were negatively related to the production accuracy, emphasizing that leftward WM asymmetry predicts successful speech sound learning (Vaquero et al., 2017).

In summary, this body of literature seems to suggest opposing roles of left versus right hemispheres. Greater leftward asymmetry of brain structure and function in the fronto-parieto-temporal regions in the left hemisphere predict more effective acquisition of foreign speech sounds. This relationship was either weaker or reversed between the brain measures in the right hemisphere and speech sound learning. These findings are consistent with the hemispheric asymmetry framework proposed for speech processing (Hickok & Poeppel, 2007, 2016). The brain correlates in the left hemisphere highlighted in this section have been associated with native speech sound perception and especially articulation. Individual variations in the structure and function of these regions might index an overall sensitivity to cross-linguistic phoneme-level differences in speech input. In contrast, the involvement of right-hemisphere homologues of these regions, such as the right temporal and parietal regions, may be limited to processing speech

inputs at a slower rate (e.g., at the syllable level). Identifying and imitating novel speech sounds relies on the mastery of fine-grained fast-sampling processing at the phoneme level, a specialization of the left hemisphere.

2.2 Neural predictors of word learning success

Word learning aims to accomplish accurate sound-to-meaning mapping, which is often comprised of two stages: identifying novel speech sounds and/or sound sequences followed by the acquisition of their associated meaning. The success of the first stage is tightly connected to speech sound learning discussed in [Section 2.1](#). Studies reviewed in the following section include training studies based on languages that contained either entirely novel ([Chandrasekaran, Kraus, & Wong, 2012](#); [Sheppard, Wang, & Wong, 2012](#); [Veroude, Norris, Shumskaya, Gullberg, & Indefrey, 2010](#); [Wong, Perrachione, & Parrish, 2007](#)) or familiar speech sounds ([Chai et al., 2016](#); [López-Barroso et al., 2013](#); [Prat, Yamasaki, Kluender, & Stocco, 2016](#); [Ripollés et al., 2014](#)). Findings from these fMRI and brain connectivity studies revealed both left-lateralized and bilaterally distributed patterns as neural predictors for successful word learning ([Fig. 2](#)).

A set of studies investigating the acquisition of artificial tonal language vocabulary in native English speakers tested whether naïve learners with greater sensitivity to foreign speech sounds were more successful word learners. These studies found that hemodynamic responses to novel phonetic features prior to learning differentiated more successful learners from less successful ones. Learners' neural activation and FC during a sublexical pitch discrimination task were examined before participating in a pseudoword learning program lasting a few weeks. Neural activation in the left inferior colliculus in the midbrain and bilateral cortical regions in the temporal lobe (superior temporal gyri (STG) and middle temporal gyri (MTG)) were associated with more successful subsequent word learning ([Chandrasekaran et al., 2012](#); [Wong et al., 2007](#)). Robust group differences between more successful and less successful learners also manifested in the FC measured across neural regions during pitch discrimination tasks. Successful learners showed increased FC across distally located brain regions at bilateral prefrontal, parietal and temporal lobes ([Sheppard et al., 2012](#)). These regions constitute critical hubs in the left dorsal auditory stream (e.g., IFG, middle frontal gyrus (MFG), and inferior parietal lobule (IPL)), as well as the right ventral auditory stream (e.g., inferior temporal gyrus (ITG)). The right

temporal regions, as discussed in [Section 2.1](#), are specialized for analyzing slower acoustic features in speech. The contribution of the right hemisphere found in these studies has been argued to be specific for processing pitch contours, such as the tonal features of a language.

The key role of the left dorsal stream in learning words containing novel phonetic features has also been confirmed in a more naturalistic learning context. Native Dutch speakers learned to recognize Mandarin words from watching weather reports in a single training session. Greater spontaneous FC between left frontal regions (precentral gyrus) and the left supplemental motor area, regions important for phonetic rehearsal, was positively associated with Mandarin word learning outcomes ([Veroude et al., 2010](#)). These findings suggest that the strength of connectivity between regions critical for speech perception and articulation in the left hemisphere may predict success in learning of novel words with high phonetic distance from one's native language.

In terms of learning novel words with a familiar speech sound system, the evidence for left-lateralized neural predictors from lab-based training studies is rather weak. Two studies investigated the acquisition of pseudowords with or without associated meaning. In one study, native Spanish speakers listened to a fluent speech stream of artificial language that were built following Spanish phonotactic constraints. While greater structural connectivity measured by radial diffusivity (RD) in the left AF predicted how well learners memorized the cooccurrence patterns of speech syllables in the pseudowords after 5 min of exposure, the relationship between the right WM tracts and the learning outcomes showed similar trends, though not statistically significant ([López-Barroso et al., 2013](#)). When learning involves meaning acquisition, the specificity of the left-hemispheric contribution becomes even less clear. Native German speakers learning to derive meaning of pseudowords from sentential context recognized more words if they had greater WM connectivity across the left AF, left uncinate fasciculus, bilateral superior longitudinal fasciculus (SLF), and bilateral inferior longitudinal fasciculus (ILF) ([Ripollés et al., 2014](#)). These findings point to a bilateral contribution to the neural preparedness for word learning and suggest that right-hemispheric involvement is not limited to tonal language learning.

Two studies addressed learners' variation in L2 vocabulary knowledge after holistic language learning and reported opposite hemispheric contributions. [Chai et al. \(2016\)](#) investigated the neural predictors of French expressive vocabulary in a group of native English-speaking learners after 12 weeks of intensive immersion training. The pre-training rsFC pattern seeded from

the left anterior insula/frontal operculum (AI/FO), a region associated with native language lexical retrieval, was positively associated with the number of words correctly produced in spontaneous speech samples. In particular, more successful learners showed greater connectivity (1) between the left AI/FO and left STG and (2) between the left AI/FO and dorsal anterior cingulate cortex (dACC) (Chai et al., 2016). The former results support the findings from the laboratory-based training studies implicating the important role of the left dorsal stream in expressive vocabulary acquisition. On the other hand, the latter finding about the connectivity between the left AI/FO and dACC, a cortical structure located between the hemispheres, suggests successful learners might be equipped with stronger functional coupling between the language network and domain-general cognitive control network (Roelofs & Piai, 2011).

By contrast, an electrophysiological study investigating the resting-state EEG indices of receptive vocabulary in a group of native English speakers found strongly right-lateralized neural correlates. EEG power measurements indexing the magnitude of neural oscillation were related to learners' receptive vocabulary at the end of training. Higher accuracy in translating French words and phrases into English was reliably predicted by greater EEG power in right frontotemporal electrode sites, and more importantly, by the degree of right laterality in EEG power (Prat et al., 2016).

To summarize, studies of neural predictors of word learning provide some support confirming the importance of the left dorsal stream (Chai et al., 2016; López-Barroso et al., 2013; Ripollés et al., 2014; Veroude et al., 2010). However, many studies do not support a specificity of left hemisphere findings and instead present evidence for a bilateral distribution of neural predictors (López-Barroso et al., 2013; Ripollés et al., 2014; Sheppard et al., 2012; Wong et al., 2007). The association between the right hemisphere and vocabulary acquisition, reported by one EEG study, is posited to arise as a factor of the degree of right laterality (Prat et al., 2016). Greater neural activation and stronger connectivity along the left dorsal stream might index strength on multiple dimensions, for instance, sensitivity to foreign speech sounds, phonological working memory, and ability to map sound onto articulation. Right-hemisphere structures, sensitive to acoustic information in speech over longer timescales (Hickok & Poeppel, 2007), may represent learners' ability to detect fine-grained acoustic differences in foreign speech sounds and access syllable-level information for lexical access in general (also see discussion on the role of the right hemisphere in holistic proficiency in Section 3.5).

2.3 Neural predictors of literacy acquisition success

The neural predictors of adult literacy acquisition have only been reported in two classroom-based training studies. In the same group of English-speaking learners of French, [Chai et al. \(2016\)](#) and [Barbeau et al. \(2017\)](#) both found functional features in the left-hemisphere prior to learning that were associated with improvement in French passage reading time across 12 weeks of training ([Fig. 3](#)). [Chai et al. \(2016\)](#) examined the rsFC seeded from the visual word form area (VWFA). The VWFA is located in the left fusiform gyrus and is implicated as a specialized structure for grapheme-phoneme mapping across different languages ([Dehaene & Cohen, 2011](#); [McCandliss, Cohen, & Dehaene, 2003](#)). Greater spontaneous connectivity between the VWFA and left STG was found to be related to greater improvement in reading time ([Chai et al., 2016](#)). The functional coupling between the VWFA and left STG has an anatomical basis: the posterior part of the left AF ([Catani, Jones, Donato, & Ffytche, 2003](#); [Catani, Jones, & Ffytche, 2005](#)). The left AF has been implicated in L1 reading ([Thiebaut De Schotten, Cohen, Amemiya, Braga, & Dehaene, 2014](#)), phonological development, and L1 literacy acquisition ([Saygin et al., 2013](#); [Yeatman et al., 2011](#)). These results suggest a shared resource for efficient grapheme-to-phoneme mapping across both L1 and L2 in the left hemisphere. Findings from [Barbeau et al. \(2017\)](#), who used a whole-brain analysis approach, were more specific to the left hemisphere. The initial neural activation in the left IPL during covert French sentence reading was predictive of reading time improvement at the end of the 12-week course. Given the fact that the left IPL is located along the superior part of the left AF and serves as an important interface between speech perception and articulation, these findings emphasized a tight relationship between L2 reading acquisition and the functional organization of the brain regions for L1 reading.

Although comprehension accuracy was not measured in these two studies, reading naturally engages both grapheme-to-phoneme mapping and the comprehension processes that rely on vocabulary (regardless of whether phonology mediates lexical-semantic access) ([Coltheart, Curtis, Atkins, & Halter, 1993](#); [Harm & Seidenberg, 2004](#)). The left IPL has indeed been found to be actively involved in word learning ([Mestres-Missé, Rodríguez-Fornells, & Münte, 2010](#); [López-Barroso et al., 2013](#); also see [Section 3.3](#) for changes in left IPL activation during reading). Further research is necessary to identify the exact role of these neural predictors in literacy acquisition, specifically regarding whether they index participants' learning profile in phonology, lexical semantics, or the mapping between phonology and orthography.

2.4 Neural predictors of grammar learning success

Artificial grammar learning (AGL) paradigms enable examination of grammar learning independent from phonology and semantics (Reber, 1967, 1989). It has been established that the neural responses to artificial grammar processing are qualitatively similar to grammatical processing in natural languages (Petersson, Folia, & Hagoort, 2012; Silva, Folia, Hagoort, & Petersson, 2017). In particular, studies consistently found left IFG activation in artificial syntax processing (see Folia, Uddén, De Vries, Forkstam, & Petersson, 2010 for a review). However, no consensus has emerged regarding which hemisphere prior to learning explains more of the behavioral variation in AGL.

Two DTI studies investigated the structural predictors of AGL and found strikingly different results, suggesting hemispheric contributions may depend on the type of stimuli. Consistent with the role of Broca's area in artificial grammar processing, learners who showed greater connectivity in the left AF learned better when the artificial grammar was embedded in letter strings (Flöel, de Vries, Scholz, Breitenstein, & Johansen-Berg, 2009). However, when learning took place in the domain of musical pitch, greater connectivity in the right AF, instead of the left hemisphere, was associated with better AGL ability (Loui, Li, & Schlaug, 2011). Both studies based their lateralization findings on a comparison between the two hemispheres. The specific contribution of the right AF was attributed to right-lateralized pitch processing (Golestani et al., 2002; Zatorre & Gandour, 2008). Paradoxically, AGL was designed to model domain-general implicit learning of grammar (Reber, 1967). It remains an open question whether the brain regions connected by these tracts subserve the computational processes underlying extraction and generalization of grammatical rules or whether they represent participants' perceptual abilities.

2.5 Neural predictors of holistic learning success

The mastery of all aspects of language will ultimately be reflected in learners' receptive and expressive language skills, often measured by holistic proficiency tests. Based on the findings on the neural predictors of language skills tested in isolation (Sections 2.1–2.4), we might expect neural features of left hemisphere or bilateral hemispheric structures to predict learners' holistic proficiency. Four studies to date have investigated the neural predictors of learners' ability to use the whole language after weeks of intensive foreign language training (Prat et al., 2016; Prat, Yamasaki, & Peterson, 2018; Qi,

Han, Garel, San Chen, & Gabrieli, 2015; Qi et al., 2019). Contrary to what was predicted, pre-training measures in the right hemisphere, rather than left hemisphere, appear to predict the ultimate attainment of holistic proficiency.

The first set of evidence comes from two electrophysiological studies which examined learners' resting-state EEG prior to 8 weeks of a French training program based on an immersive virtual reality software. EEG power measurements at the right frontotemporal electrode sites predicted both better vocabulary attainment (see Section 2.3) and faster learning rate over the course of training (Prat et al., 2016). Later analyses in a larger sample of learners replicated and extended these findings (Prat et al., 2018). Accuracy in speech production at the final stage of learning was predicted by functional connectivity between the right frontotemporal electrode sites and the degree of right laterality in EEG power.

Converging evidence for the role of the right hemisphere was provided by two classroom-based training studies using DTI and fMRI measures. Native English-speaking learners of Mandarin underwent an intensive 4-week naturalistic language course in the classroom. Learners' holistic proficiency was measured by a combination of final exam questions designed to test comprehension and production abilities in Mandarin Chinese. Measured by FA and RD, greater right hemisphere WM connectivity and greater right laterality of the tracts both predicted better final exam scores. In particular, both dorsal (superior longitudinal fasciculus) and ventral (inferior longitudinal fasciculus) tracts in the right hemisphere were associated with holistic proficiency, while no relationship was found between left WM connectivity and holistic proficiency (Qi et al., 2015). The functional role of the right hemisphere in the same group of participants was examined in a pitch discrimination fMRI task prior to training (Qi et al., 2019). Participants who showed greater right IFG engagement when discriminating pitch contours in Mandarin speech sounds scored higher not only immediately after the course, but also 3 months later without further exposure to the language. Importantly, the prediction model based on pre-training right IFG activation for the 3-month retention of Mandarin skills was verified with cross-validation methods, suggesting the model is potentially generalizable to an independent group of learners. The left hemisphere, despite its robust functional plasticity induced by training at the group level (also see Section 3.5), did not explain individual differences in holistic learning outcomes. To our knowledge, this was the first neural predictor reported for long-term retention of holistic language skills.

Together, these findings suggest that the functional and structural characteristics of the right hemisphere are major predictors of holistic proficiency attainment and retention. The observed role of the right hemisphere is unlikely to result from the unique linguistic features specific to any single second language, as French and Mandarin are distinctive across phonology, vocabulary, grammar, and orthography. This language-general account of right-hemisphere contribution has been further supported by a follow-up analysis in [Qi et al. \(2019\)](#). Pre-training right IFG activation was also strongly related to participants' foreign language learning aptitude, a composite measure of phonetic coding, grammatical ability, rote learning and rule induction (MLAT, [Carroll & Sapon, 2002](#)). The right dorsal and ventral structures highlighted in these studies have all been implicated in speech sound learning ([Golestani et al., 2002](#)), word learning ([Ripollés et al., 2014](#)), and grammar learning ([Loui et al., 2011](#)) reviewed in previous sections. However, the lack of left hemisphere findings predicting learners' holistic proficiency was unexpected, given the findings for isolated language outcomes outlined in previous sections. Holistic proficiency measures how effectively and smoothly one can integrate linguistic knowledge across phonology, semantics, syntax, and orthography domains. The variations in holistic proficiency seen here may more accurately reflect the extralinguistic skills, such as motivation, attention, memory, and cognitive control, rather than the sum of the linguistic learning skills across each domain (also see [Section 4.2](#) for discussion on the effect of training contexts and training duration).



3. Neural plasticity in successful language learning

While the previous section focuses on neural predictors of successful language learning, the current section focuses on integrating literature to illustrate the nature of the neural plasticity that is associated with successful learning of these language skills. Overall, findings across these studies emphasize the involvement of both the right and left hemispheres, whose levels of involvement tend to vary by the type of learning outcome measure ([Fig. 5](#)). The localizations of the neural plasticity findings from the structural and functional MRI studies are plotted on [Fig. 6](#) and those from the connectivity studies on [Fig. 7](#). Specifically, the majority of speech sound and grammar learning studies highlight the importance of left-hemisphere and bilateral brain plasticity, while word learning and holistic proficiency measures are most often correlated with changes in the right hemisphere. Importantly, these right hemisphere findings tend to occur in the same

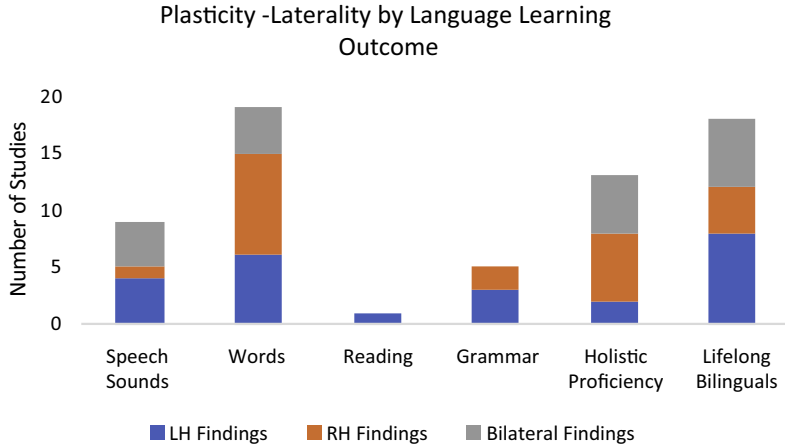


Fig. 5 Summary of laterality findings for each language learning skills where change of neural measures over the course of learning is related to learning outcomes. Abbreviations: LH, left hemisphere; RH, right hemisphere.

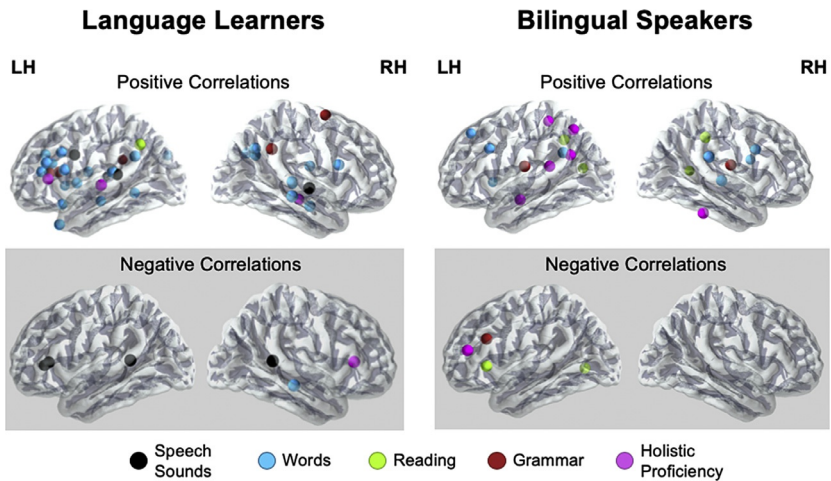


Fig. 6 Neural regions where changes in MRI measures over the course of learning was related to language learning outcomes. Top panel indicates changes at brain regions were positively correlated to learning outcomes. Bottom panel shaded in gray indicates changes in brain regions were negatively correlated with language learning outcomes. Abbreviations: LH, left hemisphere; RH, right hemisphere.

counterpart regions as those found in the left hemisphere, and the functional and structural connectivity between these right and left regions tends to also correlate with various language learning outcomes, suggesting the importance of interhemispheric dialogue for effective language learning.

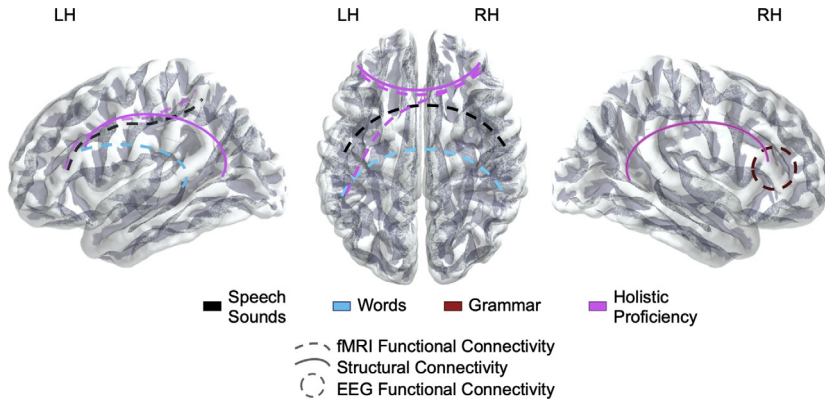


Fig. 7 Schematic showing the location of the connectivity plasticity findings in each hemisphere that were associated with language learning outcomes. Abbreviations: LH, left hemisphere; RH, right hemisphere.

Below, we discuss these brain-behavior relationships and compare them to the bilingual literature, when applicable.

3.1 Neural plasticity associated with speech sound learning

Laboratory-based phonetic training reshapes how adults perceive, categorize and produce novel speech sounds. We surveyed phonemic training studies on lexical tones and consonant contrasts. The overall findings suggest that both left and right hemispheres are sensitive to training experiences. The functional organization of left inferior frontal regions is particularly related to this learning outcome.

Studies investigating tonal speech sound learning found evidence for neural plasticity in both hemispheres. For example, Wang, Sereno, Jongman, and Hirsch (2003) examined neural activity patterns in native English speakers before and after phonemic training on Mandarin tone identification. Participants showed increased activation in the right IFG in response to Mandarin tones suggesting increasing sensitivity to acoustic pitch information (Zatorre, Evans, Meyer, & Gjedde, 1992). Further, more successful Mandarin tone learning was associated with increased expansion of neural activity in the left superior temporal gyrus (STG), a structure specialized in processing acoustic differences across phonological categories (Zatorre & Gandour, 2008). Using a sound-to-word mapping paradigm, Deng, Chandrasekaran, Wang, and Wong (2018) trained a group of native English speakers to learn a set of artificial monosyllabic vocabulary containing Mandarin tones. After training, participants who

identified tone categories more accurately showed greater FC strength between the right and left STG during the same task. Interestingly, the brain-behavior relationship existed only after learning took place in a multi-talker context, not in a single-talker context, suggesting increased interhemispheric communication might underlie effective phonetic category learning when filtering category-irrelevant talker information was necessary.

Studies of individuals learning Hindi dental and retroflex consonant contrasts have emphasized a role of the left hemisphere in successful speech sound learning. However, findings are mixed regarding the directions of these brain-behavior correlations. In a group of native Spanish speakers learning to identify Hindi dental and retroflex consonants over six sessions of phonemic training, fMRI activation in an explicit consonant category identification task was examined before and after training. Although both left and right IFG showed increased activation after training, improvement on the behavioral consonant identification test was only related to increased post-training activation in the left IFG. Moreover, intrinsic rsFC between the left IFG and the left superior parietal lobe (SPL) decreased with language training, and, importantly, this decrease in FC was correlated with better performance on the consonant identification test (Ventura-Campos et al., 2013). In a group of English speakers learning Hindi consonant contrasts in a passive listening task, less left IFG engagement in speech discrimination after training was associated with greater learning success (Myers & Swan, 2012). The negative relationship between left IFG activation and phonemic category learning success was at odds with the fMRI finding in Ventura-Campos et al. (2013), but consistent with their resting-state connectivity findings. It is likely that the opposite IFG-behavior relationships between the two studies are related to the explicit versus implicit nature of the fMRI tasks. Left IFG activation also indexes the degree of mental engagement in a cognitively demanding task. The reduced left IFG involvement in a passive listening task, together with reduced spontaneous connectivity between left IFG and left SPL, suggest more successful learners relied less on explicit perceptual categorization (Myers & Swan, 2012). Consistent with this neural efficiency account, an fMRI study investigating imitation of Hindi consonant contrasts in a group of native German speakers found a similar negative relationship between left IFG activation and participants' accuracy of imitation (Reiterer et al., 2011).

The relationship between speech sound learning and neural plasticity has also been investigated by a MEG study. MEG was recorded in an auditory

oddball task before and after a group of native Japanese speakers underwent 12 sessions of phonemic training on English /r/-/l/ categorization. Learners showed a mismatching field (MMF) increase in response to differences between consonant categories only in the left hemisphere. Moreover, learners' neural efficiency during passive listening (measured by equivalent current dipole) increased at bilateral inferior parietal regions. Learners' improvement in phonemic categorization was positively associated with greater increase in MMF as well as greater increase in neural efficiency (Zhang et al., 2009).

In sum, this line of research emphasizes the involvement of both the left and right hemispheres in successful learning of speech sounds. Speech sound learning performance was found to be related to increased neural activation and connectivity in bilateral temporal regions (Deng et al., 2018; Wang et al., 2003) and increased neural efficiency (Zhang et al., 2009) in bilateral parietal regions. These findings provide evidence for an active engagement of the right temporoparietal network in processing newly learned speech sound categories.

Collectively, these studies also suggested that functional plasticity in left frontal regions underlies individual differences in speech sound learning. However, the particular role of the left frontal plasticity remains an open question, as seen by the discrepancies in results by Ventura-Campos et al. (2013) versus Myers and Swan (2012), as discussed above. It has been proposed that left IFG engagement in speech sound processing might be limited to an earlier stage of learning, when categorical perception requires more deliberate effort. Therefore, reduced engagement of the left IFG and reduced connectivity of the left frontoparietal network might reflect the degree of automatic processing of the newly learned speech sounds in speech (Myers, 2014). Future research is necessary to dissociate the effect of learning and the effect of task demand/engagement on the functional plasticity of the left frontoparietal network, which is crucial for both speech perception as well as central executive function (Raichle, 2011; Yeo et al., 2011).

3.2 Neural plasticity associated with word learning

This section will review findings on post-training neural measures that were associated with successful word learning performance. Similar to Section 2.2, we also organize the sections into two parts, with the first focusing on word learning that involves the acquisition of a novel phonetic

category and the second focusing on word learning in a speech sound system similar to the learners' first language. Evidence from this line of research largely supports the dorsal and ventral functional framework of the language system, in which the dorsal stream is highly important for learning and retrieving the sounds of new words while the ventral stream plays a role in effective lexicosemantic access [Hickok and Poeppel \(2004, 2007\)](#). Nevertheless, the laterality of these findings is less consistent.

When new words are presented together with a novel phonetic category, learners' brain changes reflect two simultaneous experiences: speech sound learning and meaning acquisition. Studies investigating the acquisition of artificial tonal language vocabulary in native English speakers highlighted the key role of the left STG as a functional marker for word learning success. Learners who successfully integrated novel lexical tones into words are characterized by greater post-training responses to lexical tones in the left STG, while less successful learners showed greater activation in the right superior temporal sulcus (STS) and right IFG ([Wong et al., 2007](#)). The association between increased activation in the left STG and word learning success has been replicated in a few recent studies using a similar word learning procedure ([Yang, Gates, Molenaar, & Li, 2015](#); [Yang & Li, 2019](#)). These findings provided critical evidence for how superior speech perception skills might mediate successful word learning and are in line with the neural correlates of speech sound learning success reviewed in [Section 3.1 \(Deng et al., 2018; Wang et al., 2003\)](#).

Plasticity of brain structures and spontaneous connectivity patterns over bilateral frontoparietal structures after language learning also serve as important factors for word learning outcomes. After 2 weeks of training on Mandarin vocabulary, native English speakers who attained more words showed greater increase in cortical thickness (CT) in the left IFG compared to less successful learners. In the right hemisphere, localization of the structural correlates was context-specific. Better word learning was associated with increased CT in right IFG when learning took place in a traditional paired-association paradigm, and with increased CT in right IPL when learning took place in a naturalistic virtual reality context ([Legault, Fang, Lan, & Li, 2019](#)). Short-term changes in rsFC patterns have been examined in a group of native Dutch speakers learning Mandarin Chinese words from short videos. Learners' success in attaining words was reflected by increased cross-hemispheric connectivity between the left and right IPL ([Veroude et al., 2010](#)). The fact that all these structures are important nodes along

the dorsal stream suggests that they may be involved in novel speech category learning, encoding of the new phonological forms, sound-to-meaning mapping, or a combination of these processes.

Examining word learning in a speech sound system similar to learners' L1 helps to dissociate word learning from speech sound learning. Two fMRI studies investigated the encoding of the phonological forms of new pseudowords without associated meanings and confirmed the role of left frontal and temporal regions in learning phonological forms. In one study, English speakers learned to segment new words from continuous speech streams solely based on syllable cooccurrence regularities and prosodic stress cues. Greater left STG activation during passive listening was related to better performance in post-training word recognition (McNealy, Mazziotta, & Dapretto, 2006). In another study, Spanish speakers learned new segmented words from a fluent speech stream (also see Section 2.2). Greater FC between the left IFG and left posterior STG during passive listening was related to better accuracy in word recognition. However, the specificity of the left hemisphere finding in this study is weak, given the laterality index was not related to the learning outcome. In particular, the frontoparietal connectivity is numerically lateralized to the right hemisphere and was also related to word learning to a modest degree (López-Barroso et al., 2013).

Research comparing word learning for cognates and noncognates provides useful clues for the exact functional role of these neural correlates. Cognates share similar phonological forms across two languages and require minimal encoding for sound-to-meaning mapping. An fMRI study following French speakers learning Spanish words found that post-training neural activation during picture-naming in the left IFG was positively correlated with accuracy for cognate words, while neural activation in the left fusiform was positively correlated with accuracy for non-cognate words (Raboyeau, Marcotte, Adrover-Roig, & Ansaldi, 2010). These findings suggest greater left IFG activation indexes more efficient retrieval of the phonological forms of the words, while greater left fusiform activation indexes more successful mapping between meaning and new phonological forms (Wheatley, Weisberg, Beauchamp, & Martin, 2005).

Research studying the retention of word meaning suggests that not only does the left hemisphere participate in the encoding and retrieval of the newly learned words, it also maintains novel vocabulary over time. For example, German speakers learned 40 pairs of pseudowords and German translation words during sleep and were tested on their subsequent semantic retrieval in an fMRI task following waking. Greater semantic

retrieval accuracy was found to be related to greater activation in the left IFG and left temporal pole, among many other brain regions including subcortical areas (Züst, Ruch, Wiest, & Henke, 2019). Hultén, Laaksonen, Vihla, Laine, and Salmelin (2010) used MEG to track the long-term neural and behavioral maintenance of word learning. In particular, they studied Finnish speakers learning novel Finnish words in lab for 3–6 days until a mastery of words was achieved. Only the frontal and temporal regions in the left hemisphere, but not those in the right hemisphere, differentiated learned versus unlearned words immediately after training. The degree of decline in the left frontotemporal neural responses to these words 1 week after training predicted long-term retention of these words 10 months later (Hultén et al., 2010). Consistent with these findings, a structural MRI study following a group of English-speaking students after 4 months of Spanish classroom training reported that longitudinal increase in GMV in the left IFG was related to learners' performance in a Spanish semantic judgment task after the conclusion of the course (Legault, Grant, Fang, & Li, 2019). In the same study, learners' Spanish word learning success was also tested with a language decision task. Increase in CT in the right MTG was found to be related to better performance. It is likely that the right ventral stream comes to play in lexical access, especially when the task does not require explicit semantic retrieval (Hernandez, Woods, & Bradley, 2015; Rodríguez-Fornells, Cunillera, Mestres-Missé, & de Diego-Balaguer, 2009).

To summarize, the studies reviewed in this section provided some confirmatory evidence for the important role of the classic language network in the left hemisphere for word learning. In particular, the dorsal stream, including the IFG, IPL, and posterior STG, has been implicated in successful word learning involving speech sound learning and successful encoding of phonological forms. The ventral stream, including the fusiform, MTG, and the temporal pole, has been implicated in successful meaning retrieval. However, there are also substantial data supporting word-learning-related plasticity in bilateral cortical structures and in the right hemisphere. Whether the engagement of the right hemisphere is specific to language, task, or learning context requires further research.

The word learning literature thus far has mostly focused on concrete noun learning, which is only the tip of the iceberg. Additional research is necessary to understand the neural differences in the learning mechanisms between nouns and verbs, between concrete words and abstract words, and between content words and function words. For example, it has been

found that fast mapping of a meaning associated with a new noun engages the left fusiform, while fast mapping of a meaning associated with a new verb engages the left IFG and STG (Mestres-Missé et al., 2010).

3.3 Neural plasticity associated with literacy acquisition

The association between the functional plasticity of the reading network and adult learners' improvement in reading examined in Barbeau et al. (2017) corroborated their findings about the predictive role of the left IPL in reading skill acquisition (discussed in Section 2.3). fMRI during French paragraph reading in a group of English-speaking learners of French was collected before and after intensive classroom instruction lasting 12 weeks. After training, participants showed a specific enhancement of their neural response during French reading in the left IPL, which was positively correlated with French reading speed (Barbeau et al., 2017). As reviewed in the previous section, the functional plasticity in the left IPL is also related to vocabulary learning (Veroude et al., 2010). It is possible that this association is partly mediated by word learning over the course of holistic language training.

The neural correlates of reading skill improvement in this study might be limited to novice readers since the majority of bilingual literature emphasizes a more distributed network correlated with reading ability, made up of both right and left hemisphere structures, including bilateral lingual gyri (Koyama, Stein, Stoodley, & Hansen, 2013), the left IFG and inferior temporal gyrus (ITG; Cao, Tao, Liu, Perfetti, & Booth, 2013), and the right IPL and MFG (Cao et al., 2013) (Fig. 6).

3.4 Neural plasticity associated with grammar acquisition

How the left and right hemispheres process newly learned grammatical information has been found to be related to learners' grammatical proficiency. Both left and right frontal regions have been highlighted in the literature, and the laterality of these findings appears to depend on the learning stages.

Electrophysiological and fMRI data collected from a group of native Dutch speakers during AGL provided converging evidence for the importance of the right hemisphere in grammar acquisition (Kepinska, de Rover, Caspers, & Schiller, 2017; Kepinska, Pereda, Caspers, & Schiller, 2017). Grammatical sentences created on the basis of an artificial grammar BROCANTO (Friederici, Steinhauer, & Pfeifer, 2002) were presented visually during the learning phase. Even before completing the first half

of training sentences, more successful learners, compared to less successful learners, showed a more robust connectivity (measured by phase synchronization at the theta frequency band) particularly among the right frontal electrode sites (Kepinska, Pereda, et al., 2017). Employing a similar learning paradigm adapted for fMRI, the same group found that highly skilled learners showed greater neural activation at right frontoparietal regions than average skilled learners during the early test phase (Kepinska, de Rover, et al., 2017). Interestingly, the neural correlates of grammar attainment shifted toward the left hemisphere at the later stage of learning. Neural activation in left IPL measured at the end of the last learning block was found to be associated with learners' grammaticality judgment performance (Kepinska, de Rover, et al., 2017).

Laterality shifts across language training phases were reported in a group of native Spanish speakers learning Basque phrases. Event-related magnetic fields (ERFs) in response to grammatical violation changes recorded by MEG changed from an initial right-lateralized pattern to a predominantly left-lateralized pattern. Data during the last phase of learning, however, hinted at bilateral hemispheric involvement (Bastarrika & Davidson, 2017).

The engagement of the left hemisphere during a later learning stage has been supported by fMRI and sMRI studies using both artificial and real languages. In a miniature artificial language learning study, more successful grammar learners showed greater neural recruitment of the left IFG. Critically, the amount of language exposure over 4 days of training was sufficient for every learner to reach at least 75% on grammatical proficiency measures (Finn, Hudson Kam, Ettlinger, Vytlačil, & D'Esposito, 2013). Gray matter volume (GMV) in the left IFG has also been found to be related to grammatical performance in a group of Japanese-speaking learners of English. Greater leftward asymmetry in the IFG was selectively associated with greater performance on an English syntactic task (Nauchi & Sakai, 2009). The left IFG has been posited to play an important role in integrating streams of information, which is necessary for syntactic processing (Abutalebi & Green, 2007; Petersson & Hagoort, 2012). These findings suggest a greater reliance on the left IFG, consistent with a native-like pattern, as grammatical proficiency increases.

Findings across these studies suggest that the neural correlates of superior grammatical skills in adult learners vary across the stage of language learning. Right frontal regions are more likely to be engaged in earlier stages of learning, while left frontal regions come to play an important role during later stages. Finally, a more integrated bilateral hemispheric involvement toward

the end stages of grammar learning is supported by the bilingual literature. It has been found that proficient bilingual speakers recruit bilateral frontal, parietal and temporal regions for efficient grammatical processing (Hanna, Shtyrov, Williams, & Pulvermüller, 2016; Tatsuno & Sakai, 2005).

3.5 Neural plasticity associated with holistic learning success

Learning a foreign language for an extended period of time significantly reshapes the functional and structural organization of the brain (Li, Legault, & Litcofsky, 2014). Studies investigating individual differences in neural plasticity underlying successful holistic language learning indicate a dynamic bilateral framework involving neural correlates within and between the two hemispheres.

Structural MRI studies emphasize the role of classic language regions in the left hemisphere for language learning success. In a group of professional interpreters, intensive language training over 3 months substantially increased the CT in the bilateral IFG, bilateral MFG and left STG. The increase in CT in the left STG was specifically related to higher proficiency (Mårtensson et al., 2012). In a group of native English-speaking learners of German, holistic proficiency after 5 months of immersive language learning experiences was related to increase in GMV in both the left IFG and the left anterior temporal lobe (Stein et al., 2012). However, these results may not be entirely generalizable since they both used a fairly small sample size and the professional interpreter population might not be representative of all learning levels.

Structural plasticity in the right hemisphere has been highlighted in a study investigating changes in GMV and structural connectivity in a group of native Japanese late learners of English. After 16 weeks of classroom-based language training, learners showed selective increase of GMV in the right IFG and increase of FA in the right dorsal (IFG-STG) and ventral (IFG-MTG) pathways. Learners' holistic proficiency was positively related to the degree of increase in both the GMV and FA measures in the right hemisphere. Importantly, they then compared these brain measures 1 year after the training program for individuals who continued language training as compared to those who discontinued their training. GMV and FA values continued to increase for those who continued training, but went back to baseline for those who discontinued their exposure to the language, providing substantial evidence for experience-dependent neuroplasticity in the right hemisphere in response to language training (Hosoda, Tanaka, Nariai, Honda, & Hanakawa, 2013). A flexible right-hemispheric network

has also been implicated in other language training studies, which reported the plasticity of the right hemisphere as a function of the exposure to a foreign language (Hisagi et al., 2016; Mamiya, Richards, & Kuhl, 2018).

A dynamic bilateral framework involving both hemispheres has been implicated in a number of studies. An fMRI study examined functional plasticity in a group of native English speakers learning Mandarin Chinese (Qi et al., 2019). Individuals' learning success after an intensive 4-week classroom-based training was strongly related to how the right hemisphere responded to Mandarin speech sounds. However, the relationship shifted from a positive to a negative relationship after training. Superior performance at the final exam was related to greater right IFG engagement before training (see Section 2.5), greater right IFG disengagement after training, as well as pre-post increase in the rsFC (both within the left frontoparietal network and between bilateral IFG). Importantly, this right-hemispheric disengagement was related to a pre-post strengthening of the interhemispheric connectivity between the bilateral IFG. These findings suggest that sensitivity to fine-grained acoustic differences in foreign speech sounds, specialized for by the right hemisphere, might provide scaffolding to naïve learners for subsequent speech sound learning that cascades to other higher-level skills. Nevertheless, as learning continues, it is necessary to tune out differences within speech categories and focus on between-category information, which is specialized for by the left hemisphere. The interhemispheric connectivity might support the right-to-left shift of function in speech perception.

Observations from DTI studies provide additional evidence for both the right-to-left shift and the important role of interhemispheric connectivity. In a group of German students learning Dutch for 6 weeks, superior performance in a cloze test, in which participants were asked to complete the words based on the discourse context of a short paragraph, was associated with greater connectivity between the right frontal and temporal regions before language learning, and with greater connectivity between the left frontal and temporal regions after language learning (Xiang et al., 2015). Another study of English-speaking learners of Mandarin Chinese found that greater increase in WM connectivity between bilateral frontal regions was related to greater holistic proficiency after 9 months of Mandarin class (Schlegel, Rudelson, & Tse, 2012).

Taken together, these findings suggest right frontal and temporal regions in novice learners might support initial learning (Hosoda et al., 2013; Qi et al., 2019; Xiang et al., 2015), while left frontal and temporal regions are important for acquiring more advanced language skills at a later stage (Mårtensson et al., 2012). The growth of proficiency and the shift of reliance

from the right to the left hemisphere might be supported by a strengthened coupling between the two hemispheres (Qi et al., 2019; Schlegel et al., 2012). The shift of laterality implicated in this body of work is similar to findings in grammar learning studies (see Section 3.4). In comparison to the bilingual literature, lifelong bilinguals speakers' proficiency has shown to be related to a more widely distributed network including bilateral frontal regions, bilateral parietal lobes, as well as right cingulate cortex (Mechelli et al., 2004; Nichols & Joanisse, 2016; Wu et al., 2019).



4. Discussion

Evidence from recent neuroimaging studies included in this review indicate that while there is confirmatory evidence for the role of the left hemisphere in various aspects of language learning, not all aspects of language learning are left-lateralized. Prior to learning, the neural characteristics of the left hemisphere predominantly predict future speech sound learning ability. However, higher-level learning tends to be predicted by a more distributed network including the right hemisphere and bilateral brain structures. Over the course of language learning, both hemispheres show structural and functional malleability. We argue that a dynamic bilateral framework involving neural correlates both within and between the two hemispheres underlies the ultimate language learning success. Across Sections 2 and 3, we discuss laterality findings based on the language outcome that was measured or tested in each study. However, there are additional factors that could have affected these brain-behavior relationships. In this section, we summarize how the relative contribution of the left versus right hemisphere is affected by the language learning content followed by a discussion on the contributions of the duration of language learning and the limitation of the current review.

4.1 Content of language learning

For speech sound learning, while prediction studies found neural features in the left hemisphere prior to training predominantly predicts speech sound learning success, neural plasticity findings emphasize the involvement of bilateral temporoparietal networks in response to speech sound training. Moreover, left frontal engagement appears to be limited to the early stage of speech sound learning.

For word learning, the findings largely confirm the dual-stream framework proposed by Hickok and Poeppel (2004, 2007), but there is a lack of

evidence for a strong leftward laterality. The structural and functional features of the dorsal stream have been reported to predict longitudinal word learning success. The plasticity of the dorsal stream has been implicated in word learning especially when it involves encoding of novel speech sound categories or new phonological forms. The plasticity of the ventral stream has been related to successful sound-to-word mapping. Although the major findings in this literature mostly focus on the left hemisphere (except for [Prat et al., 2016](#)), numerous studies reported bilateral distribution of the neural correlates and the importance of the interhemispheric connectivity between brain-region homologues.

For reading skill acquisition, evidence is limited to one longitudinal dataset that suggests a network, which spans the left IPL, MTG, and fusiform gyrus, is critical for predicting and supporting reading in a second language. However, more research is necessary to dissociate the neural correlates specific to word comprehension versus grapheme-to-phoneme mapping.

Grammar learning and holistic language learning outcomes provide the most divergent findings across studies. For example, the left and right AF selectively predict artificial grammar learning outcomes in linguistic and musical domains, respectively. Notably, only the pre-training structural and functional features of the right hemisphere are found to predict whole-language learning success. Importantly, both lines of neural plasticity research point to a dynamic bilateral framework that shifts from a rightward to a leftward functional organization as learning advances. During the early stages of learning, right frontal regions are more engaged in grammatical processing, while during the later stages of learning, the left frontal regions become more actively engaged. A similar shift from right to left was found for the neural correlates of holistic proficiency. Structural and functional connectivity studies suggest a strengthened interhemispheric coupling resulted from holistic language training.

Taken together, these findings based on individual difference analyses confirmed that the classical language network, the processor for one's native language, explains some of the variation across adult learners in all aspects of language learning. These findings also present a wide range of brain regions in the right hemisphere, the neural characteristics of which are associated with language learning success as well, particularly during the early stage. One key question about hemispheric functional organization in language is whether the two hemispheres work in a parallel, complementary, or competitive fashion. A meta-analysis based on 128 fMRI studies ([Vigneau et al., 2011](#)) suggested that the right hemisphere works in an interhemispheric

manner during language-related tasks, as reflected via a bilateral pattern of activation, whereas the left hemisphere showed a distinctly unilateral pattern of activation. Studies using structural and functional connectivity approaches found evidence of inter-hemispheric connectivity as another critical marker of language learning success. As learning progresses, the wiring between the two hemispheres strengthens and learners rely less on the right hemisphere for language processing. These findings provide additional evidence for a model in which cross-hemispheric connectivity serves as means for contralateral inhibition and is necessary for left lateralization of language functions (Bitan, Lifshitz, Breznitz, & Booth, 2010; Hinkley et al., 2016).

4.2 Effects of training duration on language learning lateralization

So far, we have overviewed the individual differences in brain measures that are associated with language learning. However, it is also important to consider the contributions of differences in training duration across these studies. Previous models of neuroplasticity induced by bilingual experiences emphasize the effects of external factors such as the duration and intensity of language learning experience upon brain structure as a whole (Bates, 1999). Here, we discuss how the relationship between laterality findings and language learning performance may be influenced by training duration, and how different patterns may emerge for prediction versus plasticity studies.

Differences in language learning duration likely play a significant role in laterality findings, and vary over time across prediction and plasticity studies. Prediction studies generally indicated little to no involvement of the right hemisphere for studies lasting a few minutes to 2 weeks. These patterns indicate that learners' performance in shorter language learning programs, mostly laboratory-based, is explained by the neural variations in the left hemisphere, likely related to one's native language abilities. However, learners' performance in training programs that lasted 3 weeks to 5 months has been predicted more frequently by neural measures in the right hemisphere or bilateral structures, indicating success in an intermediate-level training program is associated with traits that are more domain-general (Fig. 8).

When examining neural reorganization in response to language learning (Fig. 9), studies lasting between 1 day and 2 weeks show a relatively balanced distribution of left, right, and bilateral involvement after language training. Training studies lasting longer than 2 weeks, often designed to train learners to learn all aspects of a whole language, indicated an increase in right hemisphere and bilateral involvement over time. However, by the time

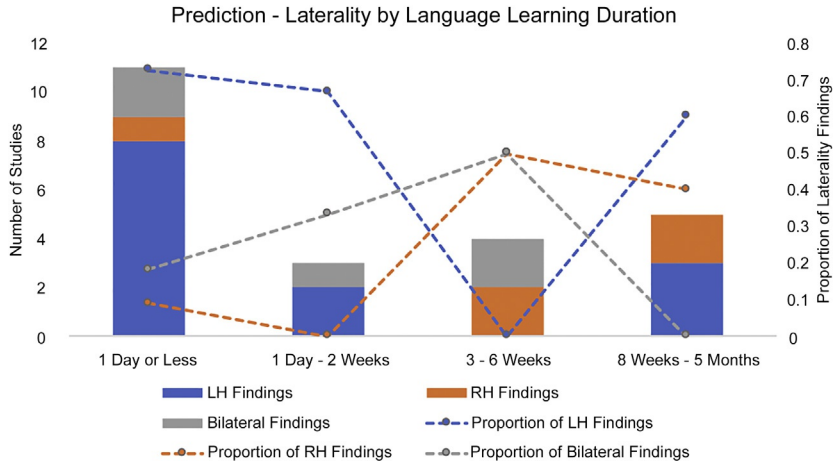


Fig. 8 Laterality findings by language learning duration for prediction-related studies. The proportion lines represent the number of left, right, or bilateral findings for each time point out of the total number of findings of that time point. Abbreviations: LH, left hemisphere; RH, right hemisphere.

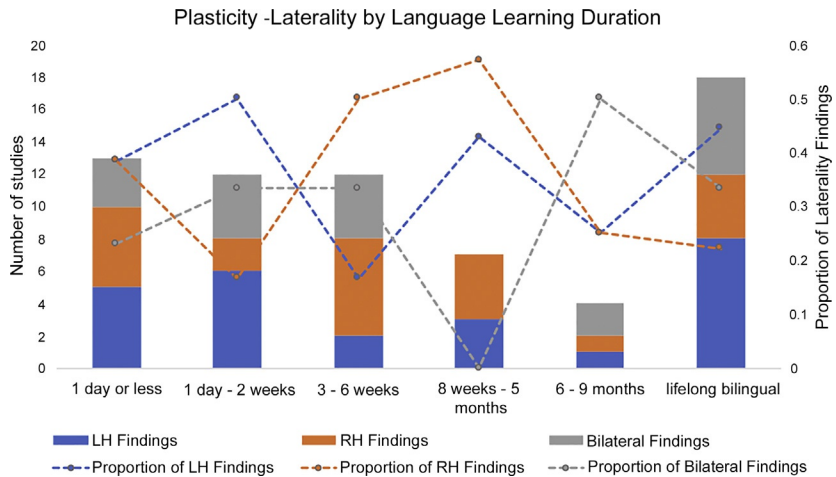


Fig. 9 Laterality findings by language learning duration for plasticity-related studies. The proportion lines represent the number left, right, or bilateral findings for each time point out of the total number of the findings of that time point. Abbreviations: LH, left hemisphere; RH, right hemisphere.

participants reached 6–9 months of language training, the laterality shifted to a predominantly bilateral and left-hemisphere reorganization in response to training. This pattern is in general consistent with the hemispheric shift from the right to left across different learning stages within learners (discussed in

Sections 3.4 and 3.5). Plasticity in the right hemisphere related to learning outcomes after an intermediate level of training (longer than 2 weeks and shorter than 6 months) might signal an acute neural reorganization in order to process unfamiliar language information. As learning duration increases from 6-month language training to lifetime bilingual experiences, familiarity to a foreign language increases as well. The proportion of reports about the neural correlates of L2 proficiency in the left hemisphere continues to increase with study duration, indicating an emergence of native-like processing in learners with higher proficiency at this stage.

4.3 Limitations

The laterality of the neural correlates reviewed in this chapter was largely determined by whether the location of the significant cluster was exclusively situated in the left hemisphere, right hemisphere, or both hemispheres. In line with the caveat we mentioned for the neuroimaging studies in native language processing in Section 1.2, many of the studies we reviewed here also only reported the localization of the neural activation/structure without (1) directly comparing the relevant importance of the two hemispheres, (2) studying the relationship between the neural measures of the two hemispheres, or (3) examining the association between laterality index and learning outcome. Therefore, the left hemisphere findings, even though prevalent across all aspects of language learning, should not be taken as direct evidence for hemispheric asymmetry in adult language learning.

Readers should also keep in mind that the current review selectively included studies that inform upon the laterality of the neural activity. Therefore, our findings are not representative of all individual difference studies of language learning, including but not limited to a large body of electrophysiological findings where neural responses during language processing are associated with learning or retention outcomes (e.g., Morgan-Short, Finger, Grey, & Ullman, 2012; Qi et al., 2017). In addition, we primarily focused on the lateralization of lateral cerebral cortical regions in this chapter. Language learning involves a distributed network that also includes the hippocampus, basal ganglia, medial cortical structures, and cerebellum (Li et al., 2014). The laterality of these structures might play important roles in adult language learning and warrant future research.

Moreover, this review does not account for individual differences due to differences in participant gender, age, handedness, or cognitive ability.

For example, while we only included studies of adult populations, the age of participants across these studies ranged from 18 to 45 years. Studies have shown that the AoA can have an effect on language learning and laterality (Johnson & Newport, 1989; Li et al., 2014); therefore, it is possible that some of the findings from studies included in this review may be mediated by AoA. Handedness has also been shown to be a factor in terms of laterality and language dominance (Knecht et al., 2000) and while the majority of studies included in this review only included right handed individuals, many did not state the criterion for handedness, and thus there could have been participants included in these studies who still had some level of left-handed use.

In conclusion, learners' native language network (reflecting a leftward functional organization for language processing) is related to learning success at the speech sound level. However, when learning involves greater complexity, the initial recruitment of the right hemisphere and the subsequent functional shift from right to left hemisphere reorganization appear to be essential to ensure successful attainment. Future work should strive to understand what cognitive and learning profiles these neural correlates actually represent.

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